THE MOLLUSCAN FAUNA OF AN UNUSUAL BERMUDIAN POND: A NATURAL EXPERIMENT IN FORM AND COMPOSITION

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ABSTRACT. Twenty-four molluscan species inhabit a landlocked marine pond of normal salinity in Hamilton Parish, Bermuda. Walsingham Pond, unusual because of its isolation and the ecologic effects thereof, can be viewed as a natural experiment. The form and composition of its molluscan fauna are compared with "control" samples from open marine environments. Composition of the fauna is similar to two modern and three fossil samples from localities similar in ecology to Walsingham Pond but directly exposed to the open sea. Isolation does not seem to affect the presence and absence of species. Walsingham Pond molluscs are, however, unique in their shell form. As demonstrated by plots of weight vs. size, the four major Pond gastropods have thinner shells than those of the same species from control samples.

It is often said that natural history is science of a lower order than experimental biology. If description and explanation are viewed as ascending orders of sophistication, this charge is valid when natural history remains at the level of "plain story"; for the very undertaking of an experiment implies a search for explanation. Yet there are a variety of natural situations that possess the essential character of experiments, even though no human manipulation of material is involved. The evolutionary phenomena of parallelism and convergence, for example, serve the same function as experimental replication; both provide the repeated occurrences upon which inductive generalizations are based (Harris and Morren, 1966). I am concerned here with another kind of "natural experiment" — the unusual situation amidst a large number of "normal" occurrences that act as controls.

Walsingham Pond in Hamilton Parish, Bermuda, is an unusual situation. Walsingham is a landlocked marine pond of nearly normal salinity maintained by tidal interchange with Castle Harbor through underground caves. Limestone walls and mangrove roots

form the borders of the Pond; the bottom is covered with a soft organic mud composed primarily of decaying material, faecal pellets, and shell fragments. Dominant elements of the bottom biota are the alga *Chaetomorpha crassa,* a profusion of sponges, and, unfortunately for collectors, the jellyfish *Cassiopeia;* there are no hard corals in the Pond. Maximum water depth is 22 feet; the bottom mud layer may be several feet thick. Helz (unpublished manuscript) studied the water chemistry of Walsingham Pond. Oxygen increases steadily from top to bottom; values are consistently 1 ml/l less than those of the normal marine waters of Castle Harbor. Nitrate and phosphate show no trend with depth; values are two to three times those of Castle Harbor. This abundance is presumably related to the continuing concentration of organic matter in Walsingham Pond. After several rainless days, Pond salinity was 100-170 ppm higher than that of Castle Harbor. Surface waters were 10-50 ppm above bottom waters; mixing may occur by sinking of the denser surface water. Ten hours after a heavy rain, surface waters of the Pond were less saline than those of Castle Harbor by 1500 ppm.

Two aspects of the Pond fauna — composition and form — may be studied to find and explain differences between this unusual situation and the normal open marine habitats of Bermuda. I have confined my attention to the Mollusca, due both to personal preference and to the availability of abundant comparative material in the magnificent collection of Mr. Arthur Haycock (Bermuda Museum). Since Walsingham Pond's landlocked status is its most unique attribute, I shall concentrate on questions related to this point. We shall want to know if the Pond's isolation, of itself, influences the form and composition of its molluscan fauna. Failing such influence, we may still ask if a secondary result of isolation — an unusual condition of water chemistry attributable to curtailed mixing of Pond with ocean, for example — can be correlated with differences between the Pond fauna and "control" faunas from normal marine environments.

COMPOSITION OF THE MOLLUSCAN FAUNA

Nine thousand two hundred fifty years ago, the sea stood approximately 78 feet below its present level (A. C. Neumann, personal communication, determined this figure by dating a peat bed cored at the bottom of Harrington Sound). With a maximum depth of 22 feet, Walsingham Pond cannot be more than a few thousand years old. Entrance to the Pond can be obtained only through the channels of underground caves that connect Walsingham to

Castle Harbor; I suspect that the molluscan populations now living in the Pond owe their origin to the infrequent transport of larvae through these channels. If this isolation exerts a major control on composition, I would expect a disharmonious assemblage of molluscan species with a predominance of forms having long and highly mobile larval stages. If ecology is the major control, then neither the young age of the Pond nor its isolation should affect the distribution of species. In this case, I would expect a molluscan fauna composed of those species that characterize similar environments in open marine areas around Bermuda. This finding would carry the implication that most molluscan species had ample access to the Pond and that the composition is a function of the normal environmental preferences of species rather than of chance introductions.

I have endeavored to compile a complete listing of the molluscs in Walsingham Pond. Shells were obtained both by visual collecting and by bulk sampling with a Van Veen grab at various depths; composition does not seem to change with depth. With the exception of *Chama macerophylla,* which occur infrequently, cemented to the limestone walls, all species inhabit the muddy bottom. Some burrow into the mud (*Vermicularia spirata*), others crawl along the surface (*Nassarius ambiguus*), and still others (*Modulus modulus*) commonly live among the algal colonies of *Chaetomorpha crassa.*

Class Bivalvia
  Family Mytilidae
      Brachidontes exustus (very few specimens)
    Condylocardiidae
      Carditopsis smithii (one specimen)
    Lucinidae
      Codakia orbiculata (most common bivalve in Pond)
    Chamidae
      Chama macerophylla (infrequently on limestone walls)
    Leptonidae
      Lasaea bermudensis (very common)
    Cardiidae
      Laevicardium laevigatum (one immature specimen)
    Veneridae
      Gouldia cerina (very common)
    Tellinidae
      Tellina mera (one specimen)
    Sanguinolariidae
      Tagelus divisus (rare)

Class Gastropoda
  Family Rissoidae
        Alvania platycephala (very common)
        Rissoina cancellata (one specimen)
      Vitrinellidae
        Vitrinella helicoidea (moderately common)
      Turritellidae
        Vermicularia spirata (most common mollusc in Pond)
      Caecide
        Caecum delicatulum (a few specimens)
        Caecum termes (very common)
      Modulidae
        Modulus modulus (very common)
      Cerithiidae
        Alabina cerithioides (quite common)
        Cerithium variabile (very common)
      Nassariidae
        Nassarius ambiguus (quite common)
      Marginellidae
        Hyalina avena (rare)
      Bullidae
        Bulla striata (rare)
      Atyidae
        Haminoea antillarum (rare)
      Retusidae
        Retusa candei (moderately common)
      Pyramidellidae
        Odostomia didyma (moderately common)

I was able to obtain samples of the molluscan fauna from five additional localities of similar environment (mangrove roots and muddy substrates), but situated in areas having free access to the open sea. These "controls" should serve to test the hypothesis that composition of the Walsingham Pond fauna is unusual for a mangrove-mud area because of the Pond's isolation and young age.

1. Ely's Harbour, Sandys Parish (grab sample collected at a depth of 10 feet by Robert F. Schmalz).

2. Mangrove root area on north coast of Ferry Reach, 50 yards east of Bermuda Biological station (personally collected; three Van Veen grab samples at depths of 5-7 feet).

Fortunately, three small samples of fossil shells were available to provide some temporal control on the stability of community composition during the past 10,000 years. Dried mud and mangrove root fragments were present in all samples.

TABLE 1

Composition and Relative Abundance of Macromolluscs in Mud-Mangrove Environments.
(Relative abundance indicated by numerical order.)

	Verticularia spirata	*Cerithium variabile*	*Codakia orbiculata*	*Modulus modulus*	*Nassarius ambiguus*	*Bulla striata*	*Tagelus divisus*	*Brachidontes exustus*	*Tellina mera*	*Batellaria minima*	*Chione cancellata*	*Columbella mercatoria*	*Cantharus tinctus*
I. Modern Samples													
Walsingham Pond	1	2	3	4	5	6	7	8	9				
Ely's Harbour	1	2	3	3	4	5	7	8					
East of Biostation	3	2	4	5	6	9	10	7		1	8	11	
II. Fossil Samples													
Pembroke Marsh	4	2	1	3	5						6		7
Longbird 4 (-71.8 feet)	2	6	3	5	4	7	8				1		
Longbird 5 (-85.5 feet)	1	5	4	3	2								

3. Pembroke Marsh, Pembroke Parish (collected by Charles Schuchert of Yale University in the 1920's). Of the five controls, only this sample cannot be identified as having been in open contact with the sea.

4. Longbird Bridge boring, 71.8 feet below present sea level.

5. Longbird Bridge boring, 85.5 feet below present sea level.

Samples 4 and 5, kindly supplied by Walter S. Newman, were obtained from the test boring made prior to construction of Longbird Bridge, St. George's Parish.

Table 1 lists all the mud-dwelling macromolluscs of Walsingham and these five localities in order of their abundance (only the rock-cementing *Chama macerophylla* is eliminated by this constraint on environment). I do not know how representative the small fossil samples are of actual diversity and abundances. The micromolluscs are not included, because several of the samples contained only the larger shells, with insufficient matrix for the screening of small species. Yet strong similarities almost surely exist between micromolluscs of Walsingham and the five controls. Several specimens of *Retusa candei*, *Caecum termes*, and *Odostomia didyma*, for example, were obtained from dried mud caking the apertures of *Vermicularia spirata* specimens in the Longbird 4 sample; all three of these micromolluscs are common in Walsingham Pond.

The similarities between Walsingham and the controls are striking. Five macromolluscs strongly dominate the Walsingham fauna — *Vermicularia spirata*, *Cerithium variabile*, *Codakia orbiculata*, *Modulus modulus*, and *Nassarius ambiguus*, in that order. Excepting the absence of *Codakia* in the Ely's Harbour sample, all of these species are present in all of the five controls. Considering the small size of several samples (20 shells in Longbird 5, for example), this correspondence seems highly significant. *Bulla striata* and *Tagelus divisus*, rare but consistently present in Walsingham, are found in three and two of the controls respectively. Of *Brachidontes exustus* and *Tellina mera*, the Walsingham "trace elements," only the first is found at one other locality.

A few unexplained discrepancies arise from species present in control samples but not in Walsingham Pond. The venerid clam *Chione cancellata* is present in three of the controls, dominant in one of these (Longbird 4) but absent from Ely's Harbour and Longbird 5 as well as from Walsingham. *Batillaria minima*, a homeomorph of *Cerithium variabile*, commonly occurs with the latter in rocky and sandy intertidal environments of the open sea (they are so associated in Castle Harbour, barely 100 yards from Walsingham Pond). *Batillaria* is absent from all but one of the

mangrove-mud environments, but dominates among the mangrove roots east of the Biostation. This might argue for atypicality of the Biostation locality, but not for a lack of correspondence between Walsingham and the other controls. While it is not especially relevant to this study, the ecologic relationship of the homeomorphs *Cerithium* and *Batillaria* is a fascinating problem.[1]

Thus, the association of *Vermicularia spirata, Cerithium variabile, Codakia orbiculata, Modulus modulus,* and *Nassarius ambiguus* in Walsingham Pond is no product of accidental access, but an expression of the normal molluscan community in mangrove-mud areas. *Vermicularia* is not often thought of as an inhabitant of muddy areas, for it usually lives cemented to hard objects in clear, open water. Olsson (1951), however, found abundant specimens on the mud flats in Tampa Bay, Florida. He described them as *Vermicularia fargoi,* but I have synonymized this species with *V. spirata* elsewhere (Gould, in press). *Tagelus divisus* prefers muddy environments (Fraser, 1967). In short, the unique isolation of Walsingham Pond is not reflected in the composition of its molluscan fauna. Characteristic species of the molluscan community that inhabits mangrove-mud areas throughout Bermuda have all become established in Walsingham Pond despite the barriers to distribution.

FORM OF THE MOLLUSCAN FAUNA

Is the form of molluscan shells in Walsingham Pond different from that of the same species in open marine habitats? If such differences are found, we may again pose the question: Is the uniqueness of Walsingham molluscs attributable to the Pond's isolation *per se* or to some secondary ecologic result of that isolation? In the first instance, isolation of a small founding population maintains the distinguishing gene frequencies present, by chance, in the founding individuals or attained, without regard to adaptive significance, by genetic drift. In the second case, an unusual condition of water chemistry or bottom ecology works its influence upon the form of shells by direct phenotypic modification. A mixed case is also likely: unusual conditions establish strong selective pressures, while isolation favors the stabilization of new genotypes by

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[1] Where they occur together, distribution is not random. Patches of 20-30 individuals of one species are often found in large tracts dominated by the other. This phenomenon is particularly well seen in Coot Pond, St. George's Parish.

removing the diluting effect of gene influx from normal populations.

When a single species differs from its "control" counterparts in a unique way, it may be difficult to distinguish among the three explanations. Walsingham specimens of *Modulus modulus* are often relatively higher than is normal for the species in Bermuda. The most spectacular modification, however, is found in *Vermicularia spirata*. This gastropod customarily begins life as a normally coiled turritellid, but later cements to a hard object and uncoils its shell. In the absence of any hard substrate on the floor of Walsingham Pond, more than 95 per cent of the *Vermicularia* shells do not uncoil at all; those that do unwind slowly and regularly without a trace of the normal attachment scar. We have here the curious case of an animal reverting, functionally, to the form and habitat of its ancestor: Walsingham *Vermicularia* construct and inhabit burrows identical to those of its coiled ancestor *Turritella*. Since the Walsingham *Vermicularia* uncoil normally when provided with hard coral substrate in a laboratory tank, this striking modification may have no genetic base other than the great phenotypic plasticity permitted by the normal genotype. I have documented this case in some detail elsewhere (Gould, in press).

When many species differ from their "controls" in a similar way, some aspect of the Pond's unique ecology is probably involved in the explanation — either directly by phenotypic modification or indirectly via selection pressures. There is one general modification that affects all the major Walsingham species: Pond shells appear to be thinner than those of the same species in open marine habitats. I tested this observation by comparing plots of combined linear dimensions vs. weight for the four most common Pond gastropods (Fig. 1) with similar plots for the same species in normal marine habitats (Haycock collection, Bermuda Museum). Use of a combined linear dimension (length plus width) provides a better measure of overall size than length alone. (In *Modulus modulus*, for example, Pond shells of a given length are generally narrower — hence lighter — than are control specimens of the same length. The lower weight/length ratios of Pond *Modulus* at a given length might be due not to shell thinness [the hypothesis to be tested] but to differences in shape between Walsingham and control shells.)

In the ideal case of isometric growth, shell weight varies directly with shell volume, and shell volume increases as the cube of a single linear dimension or an added combination of such measures (using length plus width instead of length alone will modify the

Fig. 1. The four dominant gastropods of Walsingham Pond (natural size). Upper left: *Cerithium variabile*. Upper right: *Vermicularia spirata*. Lower left: *Modulus modulus*. Lower right: *Nassarius ambiguus*.

y-intercept but not the slope of this ideal weight vs. linear dimension curve):

$$\text{weight} = b \text{ (length plus width)}^3$$

Such a curve will plot as a straight line on double logarithmic paper with a slope of 3 and a y-value of b at x = 1. This situation is closely approached in the eight plots of Figure 2: slopes vary from 2.57 to 3.53. In three of the four pairs of plots, slopes are similar for Pond and control samples (Table 2). The high slope of Walsingham *Modulus* may be an artifact of a small and incomplete size range — see Bohlken, 1962:560. Pond b-values are lower than the control parameters in each case (Table 2), but this is not significant in itself, since x = 1 mm is too distant an extrapolation from the data size range to be biologically meaningful. The important point (Fig. 2) is that for *each* of the four pairs of plots, the curve for Pond snails falls *below* that for control snails over the *entire* measured size range of the samples. (The intersection of the two *Modulus* curves at a size never reached by this species is a datum devoid of biological significance; the size range of actual data should always be specified in power function plots — see White and Gould, 1965.) At any given size for which data are available,

Pond snails are lighter than control snails in each of the four species.

Similar modification of at least four species suggests that some common factor of Pond ecology is involved as direct or indirect cause. Due perhaps to the vast accumulation of decaying organic matter in Walsingham, Pond pH is a good deal lower than normal marine values. Six measures from various depths made in June 1967 ranged from 7.6 to 7.7. There is some suggestion in the literature (Ökland, 1964: 190) that low pH might inhibit shell formation even in the presence of sufficient dissolved calcium in the water; most Bermudian waters are supersaturated with respect to calcite (Schmalz and Chave, 1963). The lowered pH may make it metabolically more difficult to deposit available calcium; a given expenditure of energy may therefore produce a thinner shell in the Pond than in open marine habitats of normal oceanic pH. (We are, indeed, dealing with a deposition phenomenon rather than subsequent shell solution in Pond snails; only uneroded snails were used in these analyses.)

TABLE 2

Reduced Data for Weight vs. Size Relationships in Four Gastropod Species: Comparison of Walsingham and Control Samples.
$$\text{Weight} = b\,(\text{Height} + \text{Width})^K$$

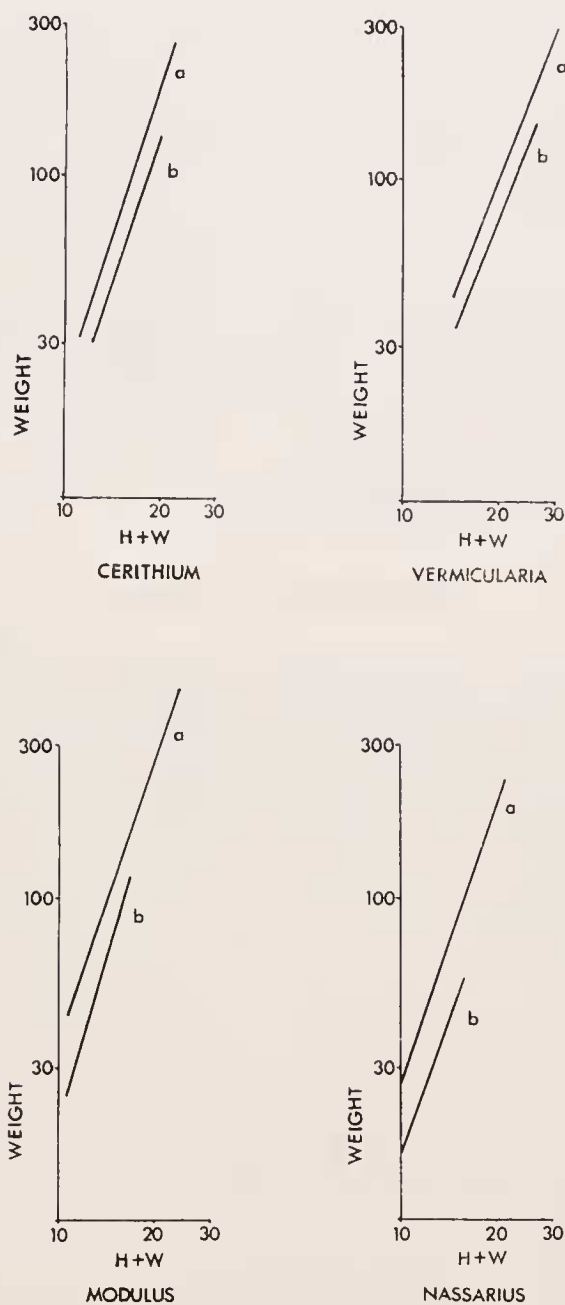|	Number of Specimens	Slope(K)	b (mm)
1. *Cerithium variabile*			
Control	20	3.24	.0123
Walsingham	10	3.14	.0115
2. *Vermicularia spirata*			
Control	20	2.65	.0356
Walsingham	15	2.58	.0348
3. *Modulus modulus*			
Control	20	3.00	.0332
Walsingham	13	3.53	.0055
4. *Nassarius ambiguus*			
Control	20	2.90	.0303
Walsingham	8	2.78	.0263

Fig. 2. Curves of weight (mg) vs. length + height (mm) for the four snails of Figure 1, both in Walsingham Pond and in normal marine habitats. Regressions marked A are for control snails, B for Pond snails. Regression lines extend only over the range of size and weight covered by actual specimens. Walsingham curves all lie below control curves, demonstrating that Walsingham shells of all species are lighter at any given weight. See Table 2 for numerical data.

I cannot state whether the thinner shells of these four species are a direct phenotypic response to unusual conditions or a result of parallel evolution, but I favor the former explanation, which is based on both the youth of Walsingham Pond and general notions of simplicity. Extreme phenotypic plasticity in shell thickness has long been recognized in land snails. By adding ground chalk to the diet of *Helix aspersa*, for example, Oldham (1934) found that shell weight increased fourfold over snails deprived of calcium.

Thus Walsingham Pond serves as a natural experiment in the form and composition of molluscan communities. The unique isolation of the Pond has no apparent effect upon the presence or absence of species but influences, in similar ways, the shell form of its dominant molluscan populations.

ACKNOWLEDGMENTS

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